

**RELATIONSHIPS BETWEEN SIZES OF MORPHOLOGICAL  
FEATURES IN WORKER HONEY BEES  
(*APIS MELLIFERA*)**

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*Abstract.*—Three important morphological attributes of 100 worker honey bees (*Apis mellifera* L.) from each of four colonies were examined morphometrically. Intertegular span (a measure of overall size), corbicular area (a measure of pollen carrying potential), and wing measurement C (highly correlated to functional proboscis length) were the morphological features selected. Worker bees with larger intertegular spans (or corbiculae, or wing measurements C) did not possess other morphological features that were highly correlated in size. This lack of correspondence was true in analyses focusing upon both linear and allometric size relationships. The lack of strong size correlations between morphological features is discussed in terms of both artificial and natural selection acting upon honey bee colonies.

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The worker honey bees (*Apis mellifera* L.) present in a colony occur in a range of sizes which, although modest compared to the intracolony worker size range of bumblebees (Plowright and Laverty, 1984), is nonetheless a significant factor in worker task performance. Among honey bees heavier foragers collect larger nectar loads, with an average ratio between load weight and unladen body weight of 82% (Wells and Giacchino, 1968). Measurements within a colony of the number of dance circuits per time indicate that larger bodied pollen foragers fly further than smaller bees (Waddington, 1988). Foragers collected from artificial feeders located at greater distances from a hive are larger than those collected at closer feeders (Waddington, 1988). Workers with larger corbiculae carry larger pollen loads back to their colony and gather more honey (Milne and Pries, 1986, 1984). Larger foragers go on more frequent foraging trips, although trip duration does not vary with body size (Cideciyan, 1984). Worker size variability among honey bees may also influence the effectiveness of dance communication (Waddington, 1989, 1988, 1981).

Larger worker honey bees might possess uniformly larger morphological features. In this case a worker with larger flight muscles would also have larger corbiculae (and hence the potential to collect heavier pollen loads) and a longer proboscis (which might improve foraging speed and breadth, as it is known to do in bumble bees (Waddington and Herbst, 1987; Plowright and Laverty, 1984; Harder, 1982; Inouye, 1980; Corbet, 1978)). However, there is reason to believe that this correspondence in sizes of morphological features might not be true in honey bees. Honey bees bred for high colonial pollen hoarding characteristics acquire larger corbiculae without larger overall body sizes (Milne et al., 1986). If artificial selection can increase the size of one morphological feature of honey bees independently of other features, is there typically any correlation between the sizes of important morphological attributes of worker bees?

In this study we selected three important morphological features of worker honey

bees, and measured the sizes of these features on 100 bees from each of four colonies. Analyses using regression techniques to examine the possibilities of either linear correlations or allometric relationships among these features (Oster and Wilson, 1978) were carried out.

#### MATERIALS AND METHODS

Four colonies of Carniolan honey bees bred from New World stocks were established in early spring using artificially inseminated sister queens. Each queen received 2 microliters of mixed semen. The semen used to inseminate each queen was taken from seven drones, each of which was produced by one of seven mother queens. The four colonies therefore each contained 7 patriline, with the greatest amount of genetic similarity possible between colonies. This was intended to reduce differences between colonies based upon patrilineal variability (reviewed in Kolmes et al., 1989).

In August, workers for morphometric analysis were shaken from the end frames of each colony into separate jars of ethanol. One hundred bees per colony were analyzed morphometrically using a Wild M5 dissecting microscope equipped with ocular micrometers. Corbicular areas were measured by multiplying their length times half of their width, using the method devised by Milne and Pries (1984). The wing measurement C of Waddington and Herbst (1987) was used as a highly correlated estimator of functional proboscis length. Intertegular span was used to measure worker size, as Cane (1987) has shown it to be a measurement free of certain complications involved in measuring dry weights (e.g., crop contents, glandular secretion storage, pollen loads). All of the 400 workers were measured for all three of the preceding morphological characteristics.

Data were analyzed using linear regression techniques. In order to determine whether corbicular areas, wing measurements C, and intertegular spans all increased or decreased in size together, pairwise linear regressions for these characteristics for the 100 workers from each hive were calculated. In order to examine the possibility of nonlinear but allometric relationships between the sizes of these morphological features, base 10 logarithms of all 1,200 morphometric values were computed and pairwise linear regression analyses for these logarithmic values for the 100 workers from each hive were calculated. This corresponds to the definition of allometric relationships given in Oster and Wilson (1978), as “. . . the sizes of two parts will be related by a simple power law:  $\log y = \log b + a \log x$ , or, equivalently,  $y = bx^a$  where y and x are linear measures of the two body parts and a and b are fitted constants the values of which depend on the nature of the measurement taken. (p. 129)”

The significances of the regression analyses were evaluated with reference to the two possible endpoints for correlations between different morphological characteristics. On one hand, there might be absolutely no relationship between the sizes of different body parts of worker bees, which is equivalent to a first null hypothesis that the sample of data was drawn from a population with a parametric correlation coefficient of zero. This was tested by comparing  $r^2$  values to tabular critical values. This procedure is preferable to evaluating the significances of the slopes of the regression lines in situations where the goal is to establish an association between variables (Keppel and Saufley, 1980).

The second possible endpoint is the case of highly correlated morphological fea-



Table 1. Mean and SE mean values for intertegular spans (mm), wing measurements C (mm), and corbicular areas (mm<sup>2</sup>) for 100 workers each from colonies 84, 85, 86, and 88.

	Mean	SE mean
Colony 84		
Intertegular span	2.93	0.017
Wing-C	3.96	0.010
Corbicular area	1.36	0.012
Colony 85		
Intertegular span	2.99	0.016
Wing-C	4.08	0.009
Corbicular area	1.42	0.010
Colony 86		
Intertegular span	3.07	0.018
Wing-C	4.06	0.012
Corbicular area	1.39	0.010
Colony 88		
Intertegular span	2.97	0.017
Wing-C	4.02	0.009
Corbicular area	1.44	0.010

tures, and here we can turn to the literature for  $r^2$  values that will make an appropriate comparison. Examples of known *Apis mellifera* morphometric features with values that are highly correlated with one another include the relationship between wing measurement C and proboscis length ( $r^2 = 50\%$ ), and the even more highly correlated relationships between head width and wing measurement C ( $r^2 = 86\%$ ) or between wing measurement A and wing measurement C ( $r^2 = 94\%$ ) reported by Waddington and Herbst (1987). Examples from other bee species include the intertegular span and dry weight linear relationship ( $r^2 = 95\%$ ) for *Diadasia rinconis* (Cane, 1987), and the correlations between wing length and proboscis length approximating 90% for four species of *Bombus* (Morse, 1977). We might expect the correlations between morphological features to be lower in honey bees than in bumble bees because of the lower variation in body size among workers of *A. mellifera* (Waddington and Herbst, 1987), but an  $r^2$  value much lower than 50% is below that which we can reasonably expect for strongly correlated morphological features even among workers of a species with a modest range of sizes. When an  $r^2$  value is much lower than these comparison  $r^2$  values, we can reject the second null hypothesis that the morphometric variables are strongly correlated to one another. The value of  $1 - r^2$  (the coefficient of nondetermination) expresses the proportion of the variation in one morphological feature that is not accounted for, or not held in common between the two variables (Keppel and Saufley, 1980).

#### RESULTS

The mean values and standard errors of the mean values for intertegular spans, wing measurements C, and corbicular areas were similar for the workers from the

Table 2. Regression analysis of morphological measures done in a pairwise fashion.

	$r^2$	Regression equation
Colony 84		
Intertegular span vs. wing measurement C	2.4%	int. = 1.84 + 0.28 wing
Intertegular span vs. corbicular area	5.9%	int. = 2.43 + 0.36 corb.
Wing measurement C vs. corbicular area	5.2%	wing = 3.70 + 0.19 corb.
Colony 85		
Intertegular span vs. wing measurement C	0.0%	int. = 3.11 - 0.03 wing
Intertegular span vs. corbicular area	0.8%	int. = 2.77 - 0.16 corb.
Wing measurement C vs. corbicular area	0.0%	wing = 4.07 + 0.01 corb.
Colony 86		
Intertegular span vs. wing measurement C	9.4%	int. = 1.11 + 0.48 wing
Intertegular span vs. corbicular area	3.3%	int. = 2.63 + 0.32 corb.
Wing measurement C vs. corbicular area	0.9%	wing = 3.92 + 0.11 corb.
Colony 88		
Intertegular span vs. wing measurement C	0.0%	int. = 2.97 + 0.002 wing
Intertegular span vs. corbicular area	2.5%	int. = 2.58 + 0.27 corb.
Wing measurement C vs. corbicular area	0.3%	wing = 4.10 - 0.05 corb.

four colonies (Table 1). The standard errors of the mean values were a small percentage of the mean values.

For none of the morphological characteristics measured was there ever a close correlation when their  $r^2$  values were evaluated with reference to  $r^2$  values for tightly correlated morphometric features (Table 2). The  $r^2$  values (expressing the strength of the correlation between the two variables being examined) ranged from 0.0% to 9.4%, with an average  $r^2 = 2.6\%$ . Even the highest  $r^2$  value indicated that the proportion of variation in one morphometric feature not accounted for (or held in common) between the two variables exceeded 90%. Therefore intertegular spans, wing measurements C, and corbicular areas did not increase or decrease together in a linear fashion among worker honey bees.

When regression analysis was carried out upon the logarithms of the morphological measurements to look for allometric relationships between body parts, the results were similar to those obtained using the untransformed data. Table 3 reports the  $r^2$  values for linear regressions carried out on log transformed data. The  $r^2$  values range from 0.0% to 9.7%, with an average  $r^2 = 2.6\%$ . Even the highest  $r^2$  indicated that the proportion of variation in one morphometric feature not accounted for (or held in common) between the two variables exceeded 90%. No reasonably strong allometric relationship between the morphological measures was apparent.

For none of the three pairs of morphometric measures (Table 2) was the  $r^2$  value averaged over all 4 colonies significantly different from that expected for a population with parametric correlation coefficients equal to zero (all  $P > 0.05$ ). Of the 12 individual  $r^2$  values for the data expressed in linear form (Table 2) evaluated for a significant deviation from  $r^2 = 0$ , in only one instance (colony 86, intertegular span vs. wing measurement C) was the difference from  $r^2 = 0$  significant at  $P < 0.01$  (df

Table 3. Regression analysis of logarithms of morphological measures done in a pairwise fashion.

	$r^2$	Regression equation
Colony 84		
Log (intertegular span) vs. log (wing measurement C)	2.5%	$\log(i) = 0.24 + 0.38 \log(w)$
Log (intertegular span) vs. log (corbicular area)	5.2%	$\log(i) = 0.45 + 0.13 \log(c)$
Log (wing measurement C) vs. log (corbicular area)	5.1%	$\log(w) = 0.59 + 0.05 \log(c)$
Colony 85		
Log (intertegular span) vs. log (wing measurement C)	0.0%	$\log(i) = 0.50 - 0.04 \log(w)$
Log (intertegular span) vs. log (corbicular area)	0.7%	$\log(i) = 0.47 + 0.07 \log(c)$
Log (wing measurement C) vs. log (corbicular area)	0.0%	$\log(w) = 0.61 - 0.0003 \log(c)$
Colony 86		
Log (intertegular span) vs. log (wing measurement C)	9.7%	$\log(i) = 0.09 + 0.65 \log(w)$
Log (intertegular span) vs. log (corbicular area)	3.9%	$\log(i) = 0.46 + 0.16 \log(c)$
Log (wing measurement C) vs. log (corbicular area)	1.1%	$\log(w) = 0.60 + 0.04 \log(c)$
Colony 88		
Log (intertegular span) vs. log (wing measurement C)	0.0%	$\log(i) = 0.47 + 0.01 \log(w)$
Log (intertegular span) vs. log (corbicular area)	2.5%	$\log(i) = 0.45 + 0.13 \log(c)$
Log (wing measurement C) vs. log (corbicular area)	0.3%	$\log(w) = 0.61 - 0.02 \log(c)$

= 98,  $r^2_{0.01} = 6.7\%$ ). In two other instances (colony 84, intertegular span vs. corbicular area; colony 84, wing measurement C vs. corbicular area) there were differences from  $r^2 = 0$  that were significant at  $P < 0.05$  (df = 98,  $r^2_{0.05} = 4.0\%$ ), but an alpha level of 0.05 is not far from the level likely to generate spuriously significant results when this many identical statistical tests are being carried out. None of the other nine individual  $r^2$  values differed significantly from 0 (all  $P > 0.05$ ).

For none of the three pairs of logarithms of morphometric measures (Table 3) was the  $r^2$  value averaged over all 4 colonies significantly different from that expected for a population with parametric correlation coefficients equal to zero (all  $P > 0.05$ ). Of the 12 individual  $r^2$  values for the data expressed in logarithmic form (Table 3) evaluated for a significant deviation from  $r^2 = 0$ , in only one instance (colony 86, log(intertegular span) vs. log(wing measurement C)) was the difference from  $r^2 = 0$  significant at  $P < 0.01$  (df = 98,  $r^2_{0.01} = 6.7\%$ ). In two other instances (colony 84,



log(intertegular span) vs. log(corbicular area); colony 84, log(wing measurement C) vs. log(corbicular area)) there were differences from  $r^2 = 0$  that were significant at  $P < 0.05$  ( $df = 98$ ,  $r^2_{0.05} = 4.0\%$ ), but again an alpha level of 0.05 is not far from the level likely to generate spuriously significant results when this many identical statistical tests are being carried out. None of the other nine individual  $r^2$  values differed significantly from 0 (all  $P > 0.05$ ).

#### DISCUSSION

Worker honey bees with larger intertegular spans (or corbiculae, or wing measurements C) did not possess other morphological features that were highly correlated in size. This was true in terms of lacking both linear relationships between morphological attributes (Table 2) and allometric relationships between morphological attributes (Table 3). Larger worker bees are not simply uniformly scaled-up versions of smaller worker bees.

The ability of Milne et al. (1986) to select for larger corbiculae was presumably based upon this loose relationship between the sizes of various morphological features. It is probable that evolutionary flexibility is increased in a system where larger corbiculae or longer proboscises could be selected for independently by environmental circumstances. Such a system would produce a single highly adaptable worker caste, rather than the multiple physical castes based upon allometric growth that are found in the ants and termites (Oster and Wilson, 1978).

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#### LITERATURE CITED

- Cane, J. H. 1987. Estimation of bee size using intertegular span (Apoidea). *J. Kans. Ent. Soc.* 60:145–147.
- Cideciyan, M. 1984. The relationships between size and behavior in worker honey bees (*Apis mellifera*). 50 pages. M.S. thesis, University of Miami, Coral Gables, Florida.
- Corbet, S. A. 1978. Bees and nectar of *Echium vulgare*. In: A. T. Richards (ed.), *The pollination of flowers by insects*. *Linn. Soc. Symp. Ser.* 6:21–30.
- Harder, L. D. 1982. Measurement and estimation of functional proboscis length in bumblebees (Hymenoptera: Apidae). *Can. J. Zool.* 60:1073–1079.
- Inouye, D. W. 1980. The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumblebees. *Oecologia* 45:197–201.
- Keppel, G. and W. H. Saufley, Jr. 1980. *Introduction to Design and Analysis*. W. H. Freeman and Company, San Francisco.
- Kolmes, S. A., M. L. Winston and L. A. Fergusson. 1989. The division of labor among worker honey bees (Hymenoptera: Apidae): the effects of multiple patriline. *J. Kans. Ent. Soc.* 62:80–95.
- Milne, C. P., R. L. Hellmich and K. J. Pries. 1986. Corbicular size in workers from honeybee lines selected for high or low pollen hoarding. *J. Apicult. Res.* 25:50–52.

- Milne, C. P. and K. J. Pries. 1984. Honeybee corbicular size and honey production. *J. Apicult. Res.* 23:11-14.
- Milne, C. P. and K. J. Pries. 1986. Honeybees with larger corbiculae carry larger pollen pellets. *J. Apicult. Res.* 25:53-54.
- Morse, D. H. 1977. Estimating proboscis length from wing length in bumblebees (*Bombus* spp.). *Ann. Ent. Soc. America* 70:311-315.
- Oster, G. F. and E. O. Wilson. 1978. *Caste and Ecology in the Social Insects*. Princeton University Press, Princeton.
- Plowright, R. C. and T. M. Laverty. 1984. The ecology and sociobiology of bumblebees. *Ann. Rev. Entomol.* 29:175-199.
- Waddington, K. D. 1981. Patterns of size variation in bees and evolution of communication systems. *Evolution* 35:813-814.
- Waddington, K. D. 1988. Body size, individual behavior, and social behavior in honey bees. Pages 385-417 *in*: R. L. Jeanne (ed.), *Interindividual behavioral variability in social insects*. Westview Press, Boulder.
- Waddington, K. D. 1989. Implications of variation in worker body size for the honey bee recruitment system. *J. Insect. Behav.* 2:91-103.
- Waddington, K. D. and L. H. Herbst. 1987. Body size and functional length of the proboscis of honey bees. *Florida Ent.* 70:124-128.
- Wells, P. H. and J. Giacchino, Jr. 1968. Relationship between the volume and the sugar concentration of loads carried by honeybees. *J. Apicult. Res.* 7:77-82.

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